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**Postembryonic Development of the Reproductive System  
Of Female European Corn Borers**

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### Abstract

Development of the female internal reproductive organs of the European corn borer, *Ostrinia nubilalis* (Hübner) was followed from hatching to the differentiation of each definitive organ. The gonads are present at hatching and become sexually distinct in the second stadium. Each ovary consists of four polytrophic ovarioles enclosed by three epithelia. At pupation, the elongating ovarioles rupture the outer epithelium and, late in the pupal stadium, the inner epithelium degenerates, leaving the individual ovarioles surrounded only by the original middle epithelium.

During the third stadium, paired imaginal discs appear on the eighth and ninth abdominal sterna. In the fifth stadium, each pair fuses medially, and an unpaired disc develops on the seventh sternum. The latter becomes the anterior part of the median oviduct. The rudiment in the ninth segment produces the vagina and accessory glands. The one in the eighth segment produces the bursa copulatrix, spermatheca, seminal duct, vestibulum, and the posterior part of the median oviduct. The vestibulum is defined as that part of the egg passageway common to the median oviduct, spermathecal duct, seminal duct, and vagina.

Seventy-two hours after pupation, all parts of the reproductive structures were present and the adult system was complete.

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# Postembryonic Development of the Reproductive System of Female European Corn Borers<sup>1,2</sup>

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## Literature Review

The literature on the insect reproductive system is extensive. We have reviewed only research that deals with the morphology and development of the internal reproductive organs of Lepidoptera. Descriptive studies of external genitalia are excluded, as are papers dealing with embryology. Anatomical studies, *per se*, are included only if we feel they contribute significantly to the knowledge of lepidopteran morphology and development, or if they bear directly upon our observations.

The earliest descriptions of the reproductive system of Lepidoptera are the classic works of Malpighi (1669) and Swammerdam (1738).<sup>6</sup> Lyonet (1762) published a monograph on the larva of *Cossus ligniperda* in which he discussed and illustrated a pair of *corps reniformes*. Although his description is somewhat confused, he correctly deduced them to be the larval gonads. We believe this work also marks the discovery of imaginal discs, although their significance was not realized until Weismann (1864) described their role in Diptera a hundred years later.

Herold (1815) made the first major contribution to the study of lepidopteran reproductive system development, and his work is the foundation for subsequent studies. He described the growth of the gonads, the fusion of the paired larval testes into a single organ, and the genesis of the internal tract from rudiments in the larva.

The earliest histological study we have seen is that of Meyer (1849), who compiled a fairly accurate picture of the histology of the gonads and described oöcyte and follicular growth and spermiogenesis. Bessels (1867) elaborated upon Meyer's observations, but little else appears until a series of important papers by Chlodkovsky (1880, 1884, 1885). The latter may be the first description of the monotrysian type of reproductive system.

The first in-depth studies of reproductive system morphogenesis are the works of Jackson (1890) and Verson and Bisson (1896a, 1896b). These studies are cited throughout this paper. They were soon followed by Petersen (1900, 1904), Stitz (1901, 1902), Gross (1903), Zander (1903, 1904) and Zick (1911). Between 1915 and 1929, Kuznetsov (1967) published the introduction to his work on Lepidoptera in which he reviewed and summarized the previous literature. In Russian, this useful work is largely ignored, but parts of it have been translated into English.

Important histological studies were made by Weidner (1934), Musgrave (1937), and Machida (1926). Norris (1932, 1933), Hewer (1934), and Ômura (1936, 1938a, 1938b) studied various aspects of the structure and operation of the reproductive system and Mehta (1933) and Dodson (1937) studied its development. The combined works of Florin (1945), Ammann (1954), and Brunold (1957) together give an especially thorough account of development in *Solenobia triquetrella*, and the publications of Joubert (1964a, 1964b, 1965, 1967, 1969) and Wittig (1960) are especially useful.

The reproductive system of the European corn borer larva has been described briefly by Larsson (1929) and Drecktrah and others (1966). Vukasović (1947) gave a short description of the female reproductive system, and Drecktrah and Brindley (1967) described in detail the reproductive system of the adults of both sexes. Additional observations, principally on the larval testes, have been made by Parker and Thompson (1927), Crowell (1929), Cloutier and Beck (1963), and Chaudhury and Raun (1966). However, no study has been made that traces the entire course of development of the reproductive system.

Not unexpectedly, the terminology used in the literature is somewhat inconsistent. Three distinct components of the reproductive system can be recognized in older female larvae. They are the ovaries, the genital cords, and the imaginal discs. The genital cords are the anlagen of the lateral oviducts, and although often referred to as the lateral oviducts (Dodson 1937, Joubert 1964a, 1969, Drecktrah and others 1966), they are not ducts but lumenless strands, which terminate blindly near the midline of the seventh segment. Herold (1815) called them *Faden*, but *Genitalstrang* has been widely used (Verson and Bisson 1896b, Sato 1932, Ammann 1954, Wittig 1960). From this word we have taken the term "genital cord," which we use until the time the cords develop lumina, after which we refer to them as oviducts.

The anlagen of the ectodermal portions of the reproduc-

<sup>1</sup> Lepidoptera: Pyralidae.

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<sup>6</sup> Although the research was conducted in 1971-72, it is the type that does not become outdated, and it has not been published previously.



tive system are paired invaginated thickenings of the ventral hypodermis of the eighth and ninth segments. They have been referred to by many names, but we simply designate them discs 8 and discs 9, respectively. Using Heinrich's (1919) setal map of the European corn borer, they are located between setae VII and VIII of their respective segments. No external evidence is present, and they cannot be seen in living larvae, although they can occasionally be seen through the cuticle of larger preserved larvae.

Mosher (1919), Heinrich (1919), Buligan (1929), and Caffrey and Worthley (1927) have all described the pupa of the European corn borer, and the pupae used in this study did not vary significantly from their descriptions. Although the female is slightly larger than the male, pupal sex is reliably determined only by the position of the genital openings, which appear as small, dark, mesoventral grooves in the cuticle.

In the female, segments 8 and 9 are highly emarginate ventrally. The genital opening reaches from the anterior margin of segment 9 to the posterior margin of segment 7. In the male, segment 8 is ringlike and the groove does not reach its anterior margin. Furthermore, the male genital opening is caudad of the eighth abdominal spiracle, whereas the female opening is cephalad of it. Caffrey and Worthley (1927) incorrectly position the respective openings caudad and cephalad of the seventh spiracle.

The European corn borer, like most Lepidoptera, has a ditrysian reproductive system with two external openings. The copulatory opening, the ostium bursae, is on the eighth segment and the oviporus is on the ninth segment. A thin-walled sac extends caudad from the posteriodorsal margin of the corpus bursae. Drecktrah and Brindley (1967) named this the bursal gland and stated that no similar structure had been reported in any other species. In their revision of the genus *Ostrinia*, Mutuura and Munroe (1970) illustrated the corpus bursae of specimens representing 17 of the 20 species in the genus. Within each species illustrated, at least one subspecies has a structure similar to the bursal gland of *O. nubilalis*.

## Materials and Methods

Specimens were reared at the U.S. Department of Agriculture's Corn Insects Laboratory, Ankeny, Iowa, on plugs of meridic diet (Guthrie and others 1965) in individual 3-dram shell vials at 27°C and 75 percent RH in continuous light. Under these conditions, each of the five larval stadia lasts about 3 days, and the first adults emerge about 6 days after pupation. Larvae were fixed daily, and the stage was determined by head capsule measurements so the chronological age and the stage were known for each specimen. Once pupae began to appear, each vial was examined every 15 minutes and the date and time of the larval-pupal ecdysis were recorded. Pupae, their age thus known within 15 minutes, were fixed at pupation (referred to as 0-hour pupae), at 6-hour intervals for the next 36 hours, at 12-hour intervals for the next 60 hours, and thereafter at 24-hour intervals until the adults began to emerge.

The oviporus opens into a short tube often called the vagina (Norris 1932, Swart 1966, Drecktrah and Brindley 1967). We show that this tube is a derivative of the ninth segment and, therefore, is not homologous to the vagina of other insects as defined by Snodgrass (1935). In the context of this study, we define the vagina as that part of the median egg passageway posterior to the origin of the seminal duct and spermatheca.

Petersen (1900) defined the lepidopteran vestibulum as the part of the egg passageway that receives the spermathecal and seminal ducts. This is the sense in which Norris (1932), Weidner (1934), Ammann (1954), Kéler (1963), Callahan and Chapin (1960), and Swart (1966) all use the term, but Beals and Berbercz (1976) call this area the genital chamber. We accept Peterson's definition and also show that the vestibulum is derived from the eighth segment, and its homologue in other insects is the vagina of Snodgrass (1933, 1935). Snodgrass and Petersen do not use the term vestibulum in the same way. Snodgrass uses it for a secondary external cavity above the seventh sternum of insects in which the seventh sternum extends beyond the eighth. Our use of vagina and vestibulum restricts use of median oviduct to that part of the median egg passage anterior to the vestibulum. This is contrary to many authors who use these terms to indicate the entire median egg passage.

Drecktrah and Brindley (1967) use vestibulum in a totally different context. They use it to designate an abrupt swelling at the base of the spermathecal duct where it joins the median egg passage. Eidmann (1929) and Khalifa (1950) also use the term this way. Although absent in representative Pieridae (Kuznetsov 1967) and Noctuidae (Callahan and Chapin 1960, Callahan and Cascio 1963), a similar enlargement has been reported in many species. Some authors have illustrated it without labeling it (Crawford 1971, Tedders and Osburn 1970). Others have used descriptive words such as tubercle (Joubert 1964b) or bulla (Fatzinger 1970). The most widely used designation, however, is infundibulum (Musgrave 1937, Srivastava 1960, Swart 1966, and Outram 1971), and this is the term we use here.

Specimens to be sectioned were fixed in hot (50° to 55°C) alcoholic Bouin's fixative (Davenport 1960). To facilitate fluid exchange, several prolegs were removed from the larger larvae and the pupal abdomen was severed at the second or third segment and the cremaster cut off. Specimens were stored in 70 percent ethanol. Specimens intended for dissection were fixed in the formalin-acetic acid-chloral hydrate solution of Chauthani and Callahan (1966) and stored in fresh solution. Living specimens were dissected in saline but, as no measurable differences were shown between living and fixed specimens, all measurements given herein are taken from fixed materials.

Larvae and excised organs were dehydrated in an ethanol series, cleared in toluene, and infiltrated with Paraplast® (Fisher Scientific Co., melting point 58°C) in a vacuum oven. Pupae were double-embedded in Parlodion®



(Mallinckrodt Chemical Works) and Paraplast. Sections were cut at 6, 8, or 10  $\mu\text{m}$  on a rotary microtome. They were stained regressively with Ehrlich's hemotoxylin (Humason 1967) and counterstained with eosin (Luna 1968) or an

eosin-Orange G mixture (Humason 1967). Permount® (Fischer Scientific Co.), or glycerine jelly wholemounts, were made of stained and unstained excised organs.

## Results and Discussion

In this paper, we describe the development of the female reproductive system from the time of hatching to the point at which the definitive organs can be recognized. Simple growth of an organ, once formed, is disregarded.

**First stadium:** Gonadal tissue can be recognized in sections of larvae fixed within 1 hour of hatching. The gonads are located in the fifth abdominal segment, ventrolateral of the dorsal blood vessel (fig. 1) but at this early age the sex can not be distinguished. They are about 25- $\mu\text{m}$  long and 10  $\mu\text{m}$  in diameter and consist of four to eight germ cells enclosed within a thin peritoneal sheath.

Their general structure and appearance do not differ significantly from the young gonads of other Lepidoptera (Machida 1926, Sato 1932, Lautenschlager 1932, and Wittig 1960). However, Joubert (1964a, 1965, 1967, 1969) found no sign of the gonads in either sex of *Sitotroga cerealella*, *Cadra cautella*, or *Plodia interpunctella* prior to the third stadium. A day after hatching, the gonads of the two sexes still can not be distinguished, but the sexes can be recognized by the presence in the male of an unpaired ventromedial invagination near the hind margin of the ninth abdominal segment. No such invagination is present in the female.

The anterior ends of the genital cords can usually be found by the second day of larval life. Each cord consists of a single row of cells leading caudad from the gonad. They are very thin (2 to 3  $\mu\text{m}$ ) and so difficult to trace that in no first instar could their posterior terminations be found. Possibly they are incomplete and do not reach the venter until later stages as in the case in *S. cerealella*, *C. cautella*, and *P. interpunctella* (Joubert 1964a, 1967). In these insects, the cords are not completed until the pupal stage, but Ammann (1954) and Wittig (1960), respectively, traced the completed genital cords of first instar larvae of *Solenobia triquetrella* and *Choristoneura murinana* to the venter of segment 7.

The anterior end of the genital cord appears slightly clavate, resembling the *Ausfuhrgang* of Ammann (1954) and the *proximale Endmasse* of Wittig (1960). It lies adjacent to a cluster of small undifferentiated cells visible at the base of the gonad (fig. 2). Wittig (1960) described similar cells as the *halbkreis formiger Mittelteil*, but Lautenschlager (1932) and Amman (1954) simply referred to apparently homologous cells as an undifferentiated cell mass. This cell mass is the primordium for the pedicels and calyx.

**Second stadium:** During the second stadium the gonads double in size, attaining a length of 65  $\mu\text{m}$ . By midstadium, the germ cells are grouped into four poorly defined clusters within a peritoneal sheath or ovarian sac (fig. 3). As the germ cells multiply, a few cells resembling the sheath cells

form a loose stroma between the germ cells and the ovarian sac, thus establishing the four ovarioles. The genital cords attain a diameter of 6  $\mu\text{m}$ , and their attachment to the ventral hypodermis of the seventh abdominal segment clearly is established. Each cord ends blindly laterad of the midline.

**Third stadium:** The third instar is large enough to be dissected easily. The gonads lie so close to the dorsum that they are best revealed by making an incision along the ventral midline and removing the gut. Staining is necessary to differentiate the developing ovaries from the surrounding fat body. The testes, however, are not embedded in the fat and can usually be seen without a stain.

The undifferentiated cell mass produces four short branches, the future pedicels, which are continuous distally with the young ovarioles. The proximal common base of the pedicels, the future calyx, is continuous with the genital cord. By midstadium, an ovariole and its pedicel are about 80- $\mu\text{m}$  long, and they may reach 130  $\mu\text{m}$  before the third ecdysis. As the stadium progresses, the stromal cells adjacent to the germ cells become flattened and begin to form a simple epithelium around the germ cells. This layer fully differentiates during the fourth stadium.

The most significant event in the third stadium is the appearance of the imaginal discs of the ectodermal portions of the female reproductive system. Their location has already been given. Discs 8 (fig. 4) appear a little earlier than discs 9, and the anterior pair is slightly larger throughout the course of development. In transverse sections, they measure 40- $\mu\text{m}$  wide and 15- $\mu\text{m}$  thick, or about three times the thickness of the hypodermis. A cluster of undifferentiated cells (arrow, fig. 4) sits atop each disc. Wittig (1960) described similar cells associated with the genital discs of *C. murinana*.

**Fourth stadium:** Discs 8 and 9 (figs. 5, 6) begins to invaginate toward the end of the fourth stadium, discs 8 invaginating first. The underlying cuticle does not invaginate. We rarely saw the discs through the cuticle, although Umeya (1927) reported that the discs of the silkworm are easily seen through its cuticle "with the naked eye." The undifferentiated cells on the surface of each disc give rise to a long, thin strand, which Wittig's (1960) study indicates is probably a nerve.

The ovarioles attain a diameter of 35 to 40  $\mu\text{m}$  and a length of 175 to 200  $\mu\text{m}$ . Each ovariole is surrounded by an inner epithelium, and adjacent inner epithelia are separated by a loose reticular stroma of varying thickness. Germ cells, inner epithelia, and stroma are all enclosed within the outer epithelium (fig. 9). Some small cells, possibly young follicle cells, are scattered among the larger germ cells. Machida (1926) identified follicle cells within the ovary of freshly

hatched silkworm larvae, but Wittig (1960) indicated they did not differentiate in *C. murinana* until the fourth stadium.

By the end of the fourth stadium, the genital cords are 12 to 14- $\mu$ m in diameter, nearly twice that in third instar larvae. The two genital cords may grow mesially and join, but the formation of this transverse connection varies and it is often not established until the middle of the fifth stadium.

**Fifth stadium:** This stage is a period of rapid differentiation of the ectodermal parts of the reproductive system. By mid-stadium, the disc doubled in size (fig. 7) and late in this stadium discs 8 and 9 fuse to produce medial unpaired rudiments, the vestibular, and vaginal rudiments, respectively (figs. 8, 17). The vestibular rudiment gives rise to the vestibulum, bursa copulatrix, spermatheca, seminal duct, and a portion of the median oviduct. The vaginal rudiment produces the vagina and the accessory glands.

The vestibular and vaginal rudiments open ventrally via elongate grooves. The vestibular groove is extended anteriorly and posteriorly by the progressive infolding of the hypodermis, joining the vaginal groove posteriorly. As the vestibular groove elongates, its margins fuse, thus forming a small tube just beneath the hypodermis. The central part of the vestibular groove remains open, and the tube grows anteriorly and posteriorly from the opening. The anterior growth becomes the median oviduct, and the posterior portion becomes the vestibulum. The central opening becomes the ostium bursae.

Concurrent with the closure of the vestibular groove, the anterodorsal and posterodorsal parts of the vestibular rudiment enlarge and elongate (fig. 17c). The former enlargement is the anlage of the bursa copulatrix, while the latter is the anlage of the spermathecal complex, that is, the infundibulum, spermathecal duct, spermatheca proper, and the spermathecal gland. In *O. nubilalis*, the rudiments of the bursa and spermatheca appear simultaneously, but Brunold (1957) found that, in *S. triquetrella*, the posterior spermathecal rudiment appears first, and then the bursal rudiment differentiates.

When discs 9 coalesce to form the vaginal rudiment, they do not quite join posteriorly so, from the dorsal aspect, the young vaginal rudiment resembles a fat letter Y (figs. 17b, c). The stem of the Y is directed anteriorly and open ventrally as the vaginal groove. The arms of the Y are directed posteriad. At first, open ventrally, the arms soon close to form short blunt tubes, the rudiments of the accessory glands. Their short common base is the future accessory gland duct, and it is continuous with the stem of the Y, the dorsal wall of the vaginal groove. By fusion of its margins, the vaginal groove closes, the most posterior part remaining open to form the oviporus. The infolding of the hypodermis and the fusion of groove margins proceeds anteriorly and, as previously mentioned, the vaginal groove becomes continuous with the posterior extension of the vestibular groove.

The median oviduct is derived partly from the vestibular rudiment and partly from an imaginal disc in the seventh segment. The latter, disc 7 (fig. 17b), appears late in the

fifth stadium and, unlike discs 8 and 9, is apparently unpaired. Ammann (1954), however, reported that, in *S. triquetrella*, this disc is originally paired. First seen about the time the vestibular groove begins to close, disc 7 is a broad thickening of the hypodermis just posterior to the transverse connection of the genital cords. It almost immediately flexes inward forming the oviducal groove which, compared to vestibular and vaginal grooves, is very short, broad, and shallow. The anterior margin of the infolded disc forms a solid tongue of tissue adjacent to the transverse connection of the genital cords, and the oviducal groove begins just behind this solid fold. With the growth and folding of disc 7, the genital cords are lifted above the hypodermis while the oviducal groove elongates posteriorly (fig. 17c). The oviducal groove becomes continuous with the anterior part of the vestibular groove and, with complete closure of the two, the median oviduct is established (fig. 17d). Most of these changes occur late in the fifth stadium.

Midway through the fifth stadium, the innermost stromal cells of the ovaries differentiate as another sheath, the middle epithelium. Three epithelia are now associated with the individual ovarioles. The outer, the ovarian sac of various authors, encloses the entire ovary, and the middle and inner epithelia constitute the wall of the ovariole (fig. 10).

This three-layered condition is transitory, however, for the rapidly elongating ovarioles soon rupture the outer epithelium. The middle and inner epithelia are not broken but remain intact and grow with the ovarioles, the former middle epithelium now being the outer wall of the ovariole (fig. 11). Srivastava and Srivastava (1959) also observed ovarian sac rupture in the fifth stadium of *Leucinodes orbanalis*, but Machida (1926) and Dutkowski (1969), respectively, reported that the ovarian sac of *Bombyx mori*, and *Galleria mellonella* is not ruptured until well into the pupal stadium.

Typical polytrophic follicles begin to develop in the lower portion of the ovarioles, and the pedicels develop lumina. These first appear just below the lowermost follicle and are separated from the follicles by a plug of tissue consisting of the upper end of the pedicels and some interfollicular tissue. By the end of the fifth stadium, the lumina extend into the calyces but not into the genital cords.

**Pupal Stadium:** Female reproductive system development in the pupal stadium is described in five stages by pupae 0-, 18-, 36-, 48- and 72-hours old. During the quiescent prepupal stage, abdominal segments 8, 9, and 10 begin to telescope into segment 7. This shortening of the abdomen and the growth of the rudiments result in the ectodermal parts of the system appearing at pupation as in figure 18. For a brief time the rudiments form a more or less continuous ventral groove, and a corresponding furrow (reaching from the rear of segment 7 to the front of segment 9) is formed in the pupal cuticle. The 8th and 9th sterna are so emarginate that the furrow is only about 0.2-mm long, but its position and the emarginate sterna are the characters used to identify female pupae.



The vestibular rudiment is differentiated dorsoanteriorly into the future corpus bursae and dorsoposteriorly into the primordium of the spermathecal complex. Anterioventrally, the vestibular rudiment is joined by the nearly completed median oviduct. Completion of the median oviduct occurs very near pupation because in half the 0-hour pupae, and in all 6-hour pupae, the oviducal groove and the anterior part of the vestibular groove were closed ventrally. The vaginal groove is continuous with the posterior part of the vestibular groove, and ventral closure does not occur until 6 hours after pupation. Thus at pupation, the vaginal and vestibular rudiments share a common external opening (dotted outline, fig. 18).

The ectodermally derived parts of the reproductive system are composed of a continuous epithelium 20- to 40- $\mu$ m thick, consisting of columnar cells with oval or round basal nuclei 5  $\mu$ m in diameter. The cytoplasm stains intensely with hematoxylin, and the cell boundaries and basement membrane are indistinct. A low, poorly defined brush border is found throughout the system. Most of the system is covered by a sheath of presumptive muscle tissue. This sheath is thickest (10- to 20- $\mu$ m, three to six layers of cells) around the vestibulum and vagina, but around the median oviduct and the proximal half of the accessory gland rudiment, it is only one cell thick. The basal half of the spermathecal rudiment is also covered with a thick sheath, but no such tissue exists around the distal half of either the spermathecal or accessory gland rudiments.

**18-hour pupa:** No new structures appear during the 18 hours following pupation, but several refinements are produced in those already present. The most striking histological feature in the 18-hour pupa is a well developed brush border, 3 to 5- $\mu$ m high, that lines the lumen of all the ectodermally derived organs. At 48 hours it is irregular and only about half as high, and it is not seen in the 72-hour pupa.

When the ventral groove closed 6 hours after pupation, the definitive ditrysian openings were established. The vestibulum is reduced to a small area shared by the median oviduct, ductus bursae, spermatheca, and vagina. The axes of the median egg passage and ductus bursae (dotted lines, fig. 19) cross in the vestibulum and will not be separated for another day. The spermathecal rudiment is distally bifurcated, the branches being 0.10 to 0.12-mm long and 50  $\mu$ m in diameter. The remainder of the rudiment is 0.50 to 0.65-mm long. The accessory gland rudiments are 3 to 4 times their length at pupation, and the proximal half of each rudiment is oriented transversely to the long axis of the abdomen. This transverse portion will become the accessory gland reservoir. But at this stage, the only distinction between the proximal and distal halves of the rudiment is the absence of a muscle sheath on the distal portion (fig. 19f).

With the formation of lumina, the genital cords become the lateral oviducts. The lumina first appear at both ends of the cords, at the calyces, and the junction with the median oviduct. They grow toward the middle of the cords

and, 18 hours after pupation, the lumina are complete. They are not continuous with the lumen of the median oviduct, however, but remain separated by a solid mass of cells, which persist to the 96-hour stage. The lateral oviducts consist of a simple low-columnar epithelium 10- to 18- $\mu$ m high, surrounding a lumen 12- to 18- $\mu$ m wide. The diameter of the median oviduct is 50 to 80  $\mu$ m, being widest near the vestibulum. Its simple columnar epithelium is 20 to 27- $\mu$ m high.

The ovarioles are 2.1 to 2.5-mm long, with a fairly uniform diameter of 60  $\mu$ m for most of their length. Developing follicles can be seen in sectioned ovarioles, but they are not evident in whole mounts. The epithelia of the pedicels and lateral oviducts are continuous, as are the lumina. However, the lumina of the pedicels and the ovarioles are still separated by the epithelial plug. A thin sheath surrounds the lateral oviducts and continues around each pedicel. In the vicinity of the epithelial plug, it becomes three- to four-cells thick, and then abruptly splits into two distinct simple layers, the middle and inner epithelia previously described.

Drecktrah (1966) described a single, syncytial sheath surrounding each ovariole of the adult European corn borer, and this appears to be the usual condition in adult Lepidoptera, as well as insects in general (Snodgrass 1935, Bonhag 1958, Davey 1965). But the developing ovary of the gypsy moth (Sato 1932) and the silkworm (Machida 1926) have three sheaths similar to those we have described here. Machida followed the development of the ovarioles through the pupal stadium and found that the outer covering degenerates immediately after being ruptured by the growing ovarioles. Then, late in pupal life, the inner epithelium breaks down, leaving one external covering, the original middle sheath. Surviving cells of the former inner sheath then aggregate in the constrictions between the follicles.

The fate of the inner sheath in *O. nubilalis* is much the same as described by Machida (1926) in *B. mori*. In the 96-hour pupa (fig. 12) it appears thinner, except in the innerfollicular constrictions. At 120 hours (fig. 13), which is very near emergence, the inner sheath is fragmentary, and its remnants are clustered in the constrictions. Such cell aggregations appear in the illustrations of many authors, including Drecktrah (1966), but neither their origin nor their significance is discussed. Except for extensive elongation, the ovarioles undergo no other morphological changes before emergence. Oogenesis and vitellogenesis were not studied.

**36-hour pupa:** Figures 20 and 21 illustrate the reproductive system at 36 hours. The rudimentary bursal gland is visible, and the definitive parts of the spermathecal complex are now barely evident. The bursal gland rudiment is up to 0.2-mm long. Its epithelium is uniform, consisting of columnar cells 15- $\mu$ m high, whereas the wall of the corpus bursae is thinner dorsally (8  $\mu$ m) than ventrally (27  $\mu$ m).

The spermathecal duct leads from the infundibulum to a slight dilation, the rudiment of the utriculus and lagena. The infundibulum and the spermathecal duct are well muscled, but the utricular-lagena dilation, the definitive sper-

matheca proper, has only a thin-muscle sheath, and even that is lacking on the spermathecal gland. The spermathecal gland is 3- to 4-mm long, delicate, and transparent. It is easily confused with the accessory glands that now follow the same path they do in the adult. Upon leaving the reservoirs, the accessory glands turn caudad, ventrad, and cephalad and usually reach the level of the corpus bursae before reversing their path. Their reservoirs are proximal dilations joined posteriorly to form the accessory gland duct. The accessory gland duct is well muscled, but the reservoirs have only a thin sheath and no muscle is found on the accessory glands themselves. The simple cuboidal epithelium of the reservoirs is readily distinguished from the columnar epithelium of the accessory glands and the accessory gland duct.

The vagina is about 0.4-mm long and slightly flattened for a short distance anterior to the accessory gland duct. This flattened area is possibly the first indication of the formation of the vaginal pouches. The epithelium, however, is uniform for the length of the vagina, the cells being distinctly acidophilic with centrally located oval nuclei.

In this stadium, the walls of the vestibulum (fig. 21) grow inward to separate the ductus bursae from the median egg passage. The separation is never entirely completed, and the connection that remains between the two tubes becomes the seminal duct. Seminal duct formation is rapid. It was not seen in pupae less than 36-hours old, but it was present in all 48-hour old specimens.

The lateral oviducts have shortened to 0.45 to 0.55 mm, but their diameter has doubled. The epithelium has lost the extreme basophilia that characterized it earlier, but cells for 80  $\mu$ m on either side of the partition between the lateral and median oviducts contain many highly basophilic globules.

**48-hour pupa:** The seminal duct (fig. 22) is now a small, distinct tube connecting the right ventrolateral side of the ductus bursae with the left ventrolateral side of the vestibulum. It is no more than 0.8-mm long and 60  $\mu$ m in diameter and composed of a simple layer of low-columnar cells covered by muscle continuous with the muscle sheath of the vestibulum and the ductus bursae.

The corpus bursae is 0.5 to 0.6 mm in diameter, usually spherical but sometimes dorsoventrally flattened. The frequency of this flattened condition increases with pupal age, and all 96-hour pupae had a flattened corpus bursae. Its epithelium consists of cuboidal cells dorsally and tall co-

lumnar cells ventrally. The cytoplasm is slightly less basophilic than before, and there is a low brush border. Ventrally, the epithelium forms a medial longitudinal fold that protrudes into the lumen (fig. 14). The fold is spindle-shaped and 260  $\mu$ m long by 80- $\mu$ m high. Its appearance marks the onset of the formation of the signum, the internal sclerite of the corpus bursae, which sclerotizes between 96 and 120 hours after pupation. The surface of the fold is very irregular, with many cytoplasmic protrusions, and a fine granular eosinophilic material fills the lumen of the corpus bursae.

Transverse sections reveal the first differentiation of the vaginal pouches as small dorsolateral evaginations of the vagina anterior of the accessory gland duct. The evaginations are histologically similar to the remainder of the vagina but, in the 72-hour pupa (fig. 15), the cuboidal cells and round nuclei of the pouches contrast sharply with the columnar cells and oval nuclei of the vaginal wall.

**72-hour pupa:** The last two definitive structures to appear are the U-shaped sclerite (Drecktrah and Brindley 1967) of the ductus bursae and a small spiral sclerite of the spermathecal duct. The U-shaped sclerite is first indicated by a dorsal depression of the ductus bursae near the ostium (fig. 16). Here the epithelium is columnar 20- to 25- $\mu$ m high with pical nuclei. The low columnar, or cuboidal epithelium, of the lateral and ventral walls of the ductus is only about one-third as high, and the nuclei are located basally. As the dorsal wall is further depressed, the lateral walls reflect mesially, and the lumen assumes a narrow U shape and develops a thick cuticle, the U-shaped sclerite. Simultaneously the ductus bursae develops a ventral dilation where it receives the seminal duct and, in so doing, the bursa copulatrix is completed.

Drecktrah and Brindley (1967) also described a small heavily sclerotized sublumen that traces a spiral path around the periphery of the major lumen of the spermathecal canal. A similar canal has been noted in many species, and it has been given a variety of such names as *Befruchtungskanal* (Weidner 1934), spiral fertilization canal (Callahan and Cascio 1963), microduct (Joubert 1964b, 1969), and subsidiary lumen (Swart 1966). In any case, no sign of it exists in 48-hour corn borer pupae, but at 72 hours it appears as a very small groove in the epithelium of one side of the spermathecal duct. It is not yet fully formed and can not be seen in whole mounts, but its distinctly spiral path can be easily traced in serial sections. Thus, 72 hours after pupation, all parts of the reproductive system of the adult are present and the system is complete.

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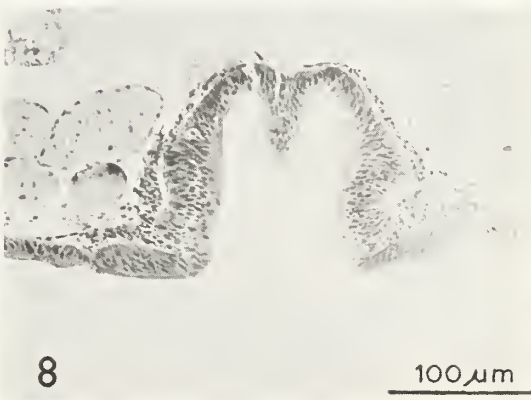
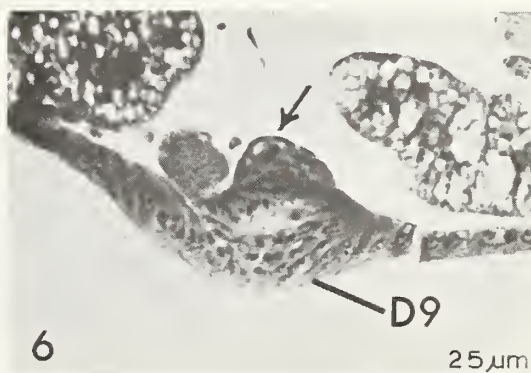
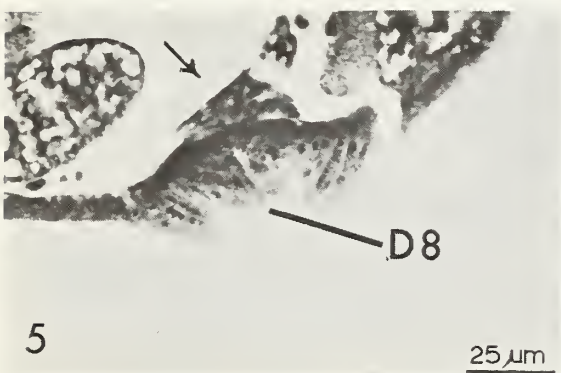
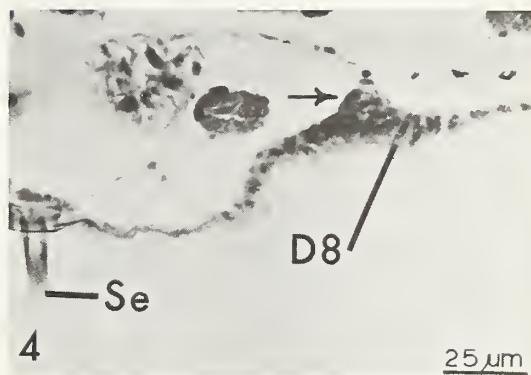
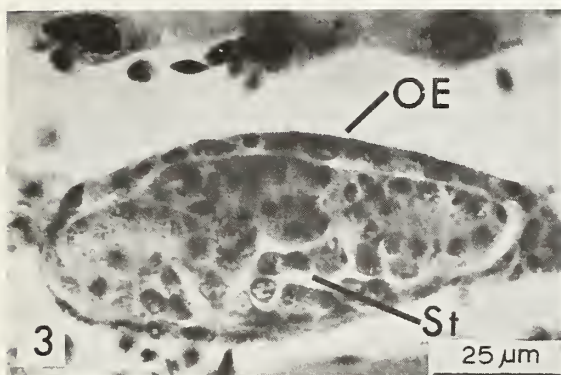
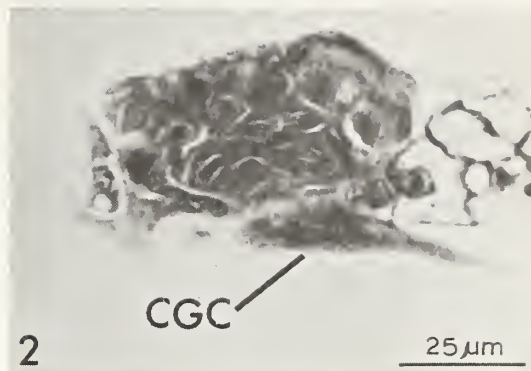


Figure 1.—Gonads, t.s., early 1st stadium. Figure 3.—Ovary, t.s., early 2nd stadium. Figure 5.—Disc 8, t.s., late 4th stadium. Figure 7.—Disc 8, t.s., mid 5th stadium.

Figure 2.—Ovary, S.S., early 2nd stadium. Figure 4.—Disc 8, t.s., mid 3rd stadium. Figure 6.—Disc 9, t.s., late 4th stadium. Figure 8.—Vestibular rudiment, late 5th stadium. Isolated rudiment, cuticle removed, showing fusion of disc 8.

Legend: CGC, clavate end of genital cord; D8, Disc 8; D9, Disc 9; DV, dorsal vessel; Go, gonad; OE, outer epithelium; Se, seta; St, stroma; arrows, undifferentiated cell mass.



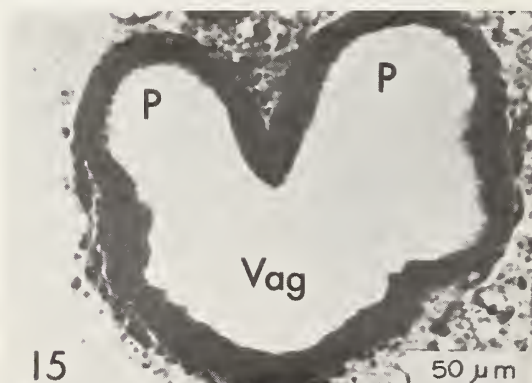
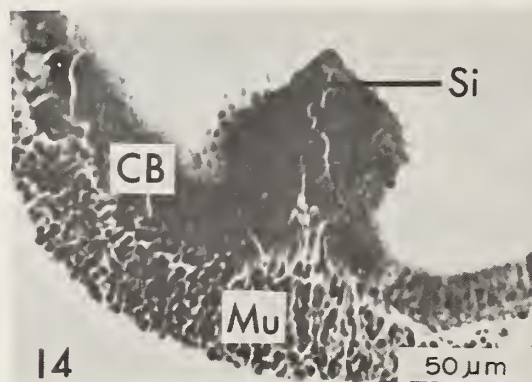
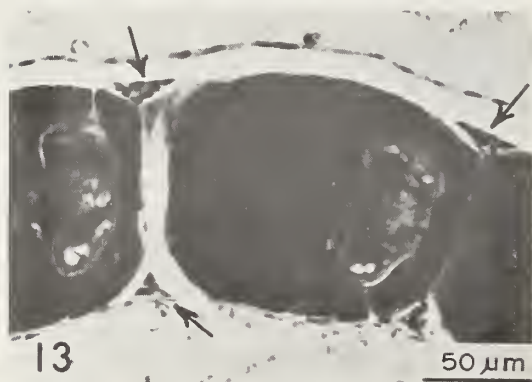
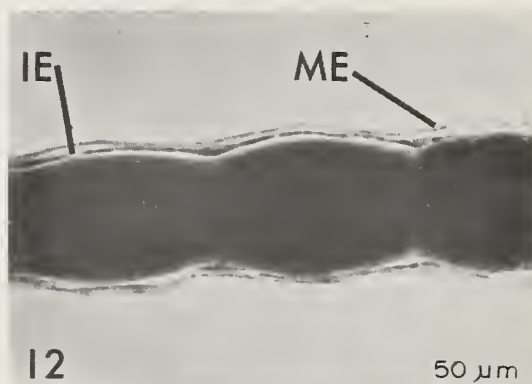
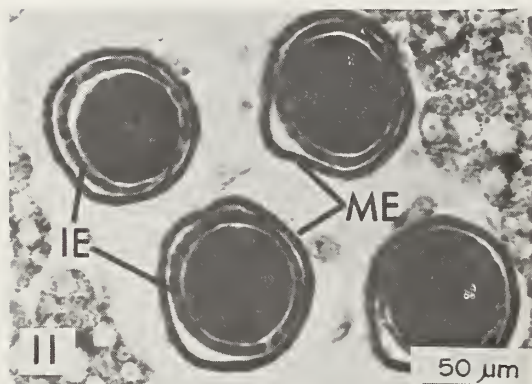
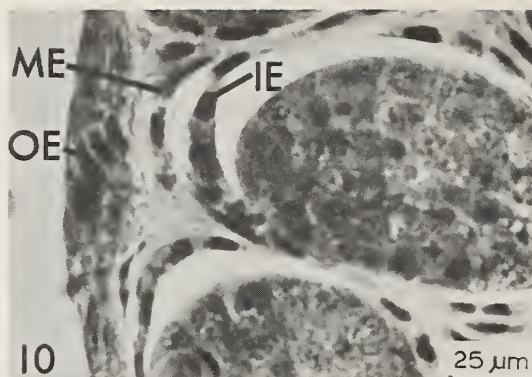


Figure 9.—Ovary, t.s., mid 4th stadium. Inner epithelium differentiating.

Figure 11.—Ovary, t.s., 6-hour pupa. Outer epithelium absent.

Figure 13.—Ovariole, t.s., 120-hour pupa. Arrows, remnants of inner epithelium.

Figure 15.—Vaginal pouches, t.s., 72-hour pupa.

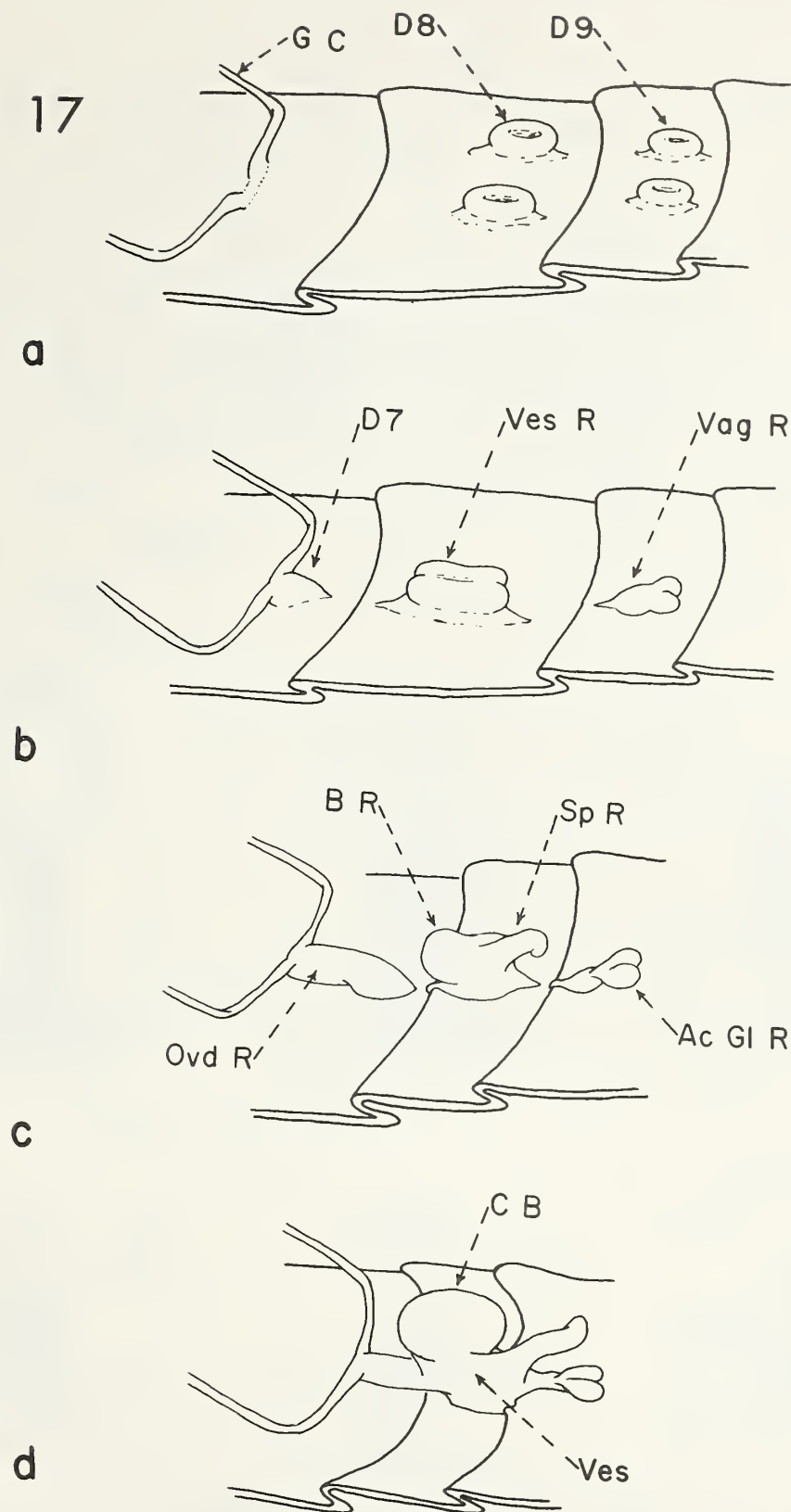
Figure 10.—Ovary, t.s., mid 5th stadium. Middle epithelium differentiating.

Figure 12.—Ovariole, w.m., 96-hour pupa.

Figure 14.—Corpus bursae, t.s., 48-hour pupa. Origin of the signum.

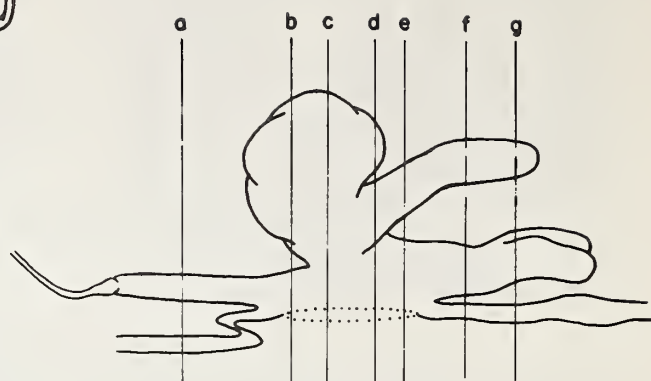
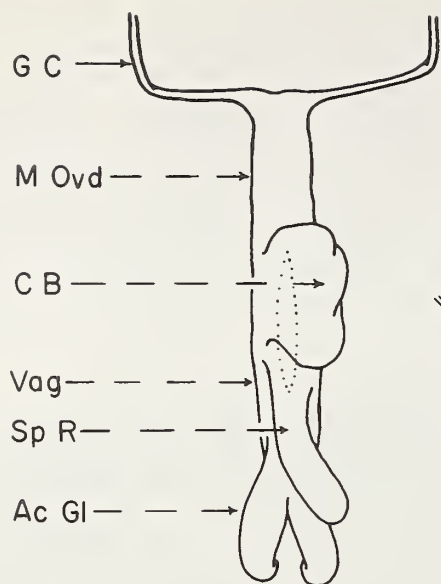
Figure 16.—Ductus bursae, t.s., 72-hour pupa. Origin of the U-shaped sclerite

Legend: CB, corpus bursae; IE, inner epithelium; ME, middle epithelium; Mu, muscle; OE, outer epithelium; P, vaginal pouch; Si, signum; St, stroma; U, U-shaped sclerite, site of; Vag, vagina.



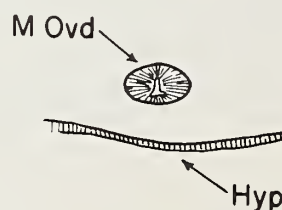
**Figure 17.**—Morphogenesis of the ectodermal portions of the female reproductive system during the 5th stadium. At the onset of the stadium (a), paired imaginal discs lie on the ventral hypodermis of segments 8 and 9. The paired discs fuse, and a median unpaired disc appears in segment 7 (b). As the abdomen shortens prior to the larval-pupal ecdysis, the rudiments in the three segments approximate (c) and form a continuous system at pupation (d).

**Legend:** AcGIR, accessory gland rudiment; BR, bursal rudiment; CB, corpus bursae; D7, D8, D9, Discs 7, 8, 9, respectively; GC, genital cord; OvdR, oviducal rudiment; SpR, spermathecal rudiment; VagR, vaginal rudiment; Ves, vestibulum; VesR, vestibular rudiment.

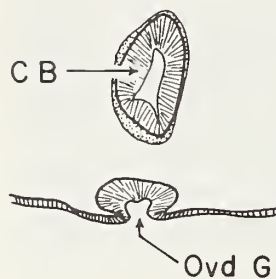


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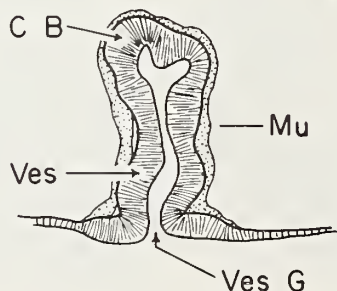
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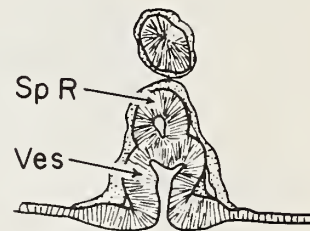
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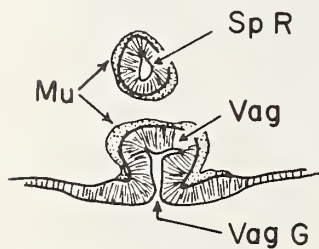
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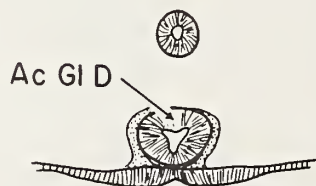
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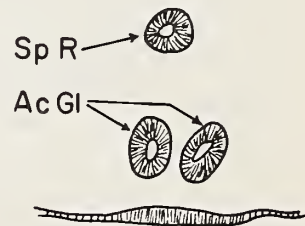
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e



f

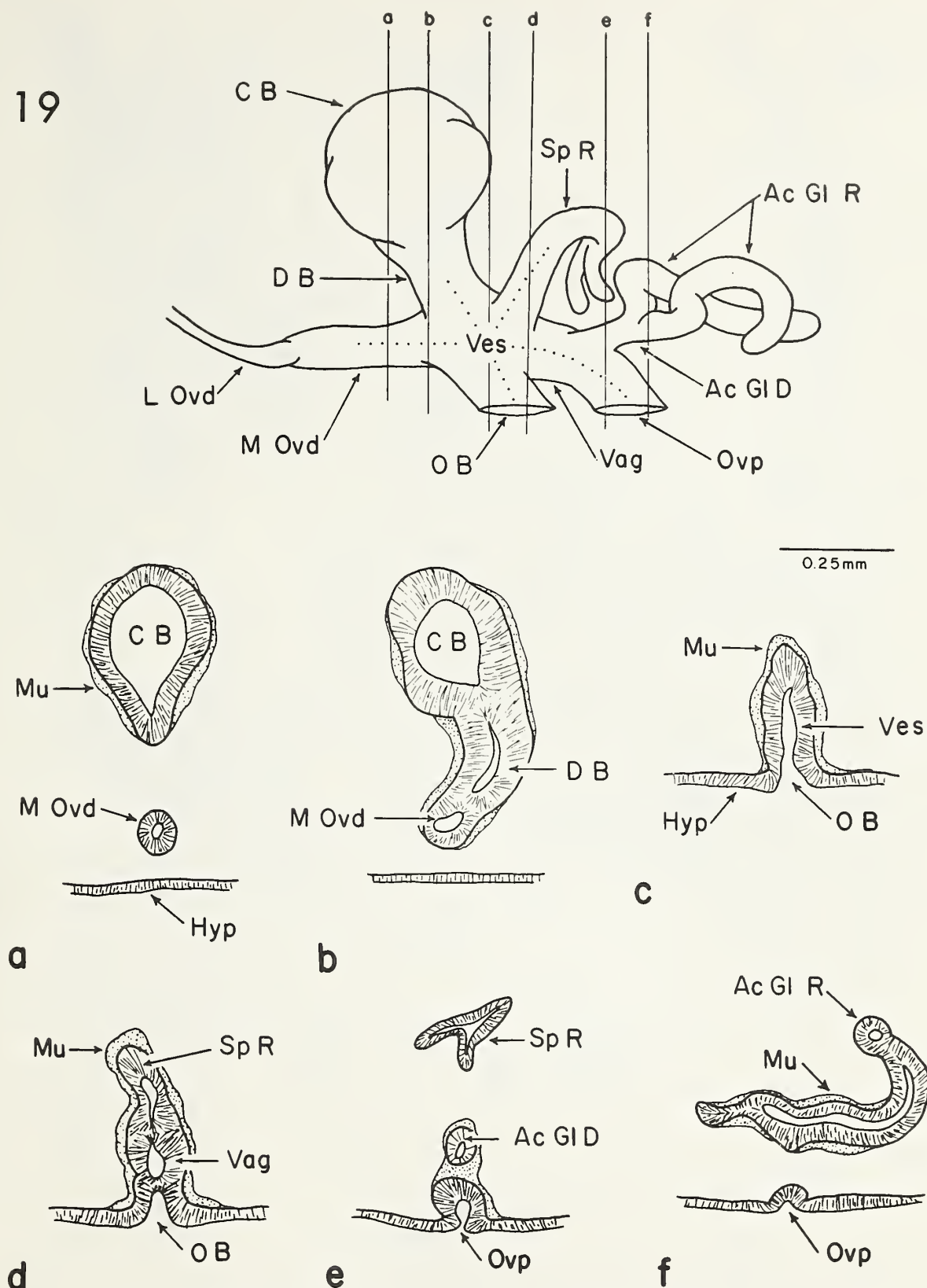


g

Figure 18.—0-Hour pupa, reconstructed from serial sections, ovaries and cuticle omitted. The dotted outline delineates the ventral groove. Lines a-g indicate the plane of the corresponding transverse sections. The outlines of the sections were traced from microprojected images.

Legend: AcGI, accessory gland; AcGID, accessory gland duct; CB, corpus bursae; GC, genital cord; Hyp, hypodermis; MOvd, median oviduct; Mu, muscle; OvdG, oviducal groove; SpR, spermathecal rudiment; Vag, vagina; VagG, vaginal groove; Ves, vestibulum; VesG, vestibular groove.





**Figure 19.**—18-Hour pupa, reconstructed from serial sections, ovaries and cuticle omitted. Lines a-f indicate the plane of the corresponding transverse sections. Outlines of the sections were traced from microprojected images.

**Legend:** AcGIR, accessory gland rudiment; AcGID, accessory gland duct; CB, corpus bursae; Hyp, hypodermis; LOvd, lateral oviduct; MOvd, median oviduct; Mu, muscle; OB, ostium bursae; Ovp, oviporus; SpR, spermathecal rudiment; Vag, vagina; Ves, vestibulum.

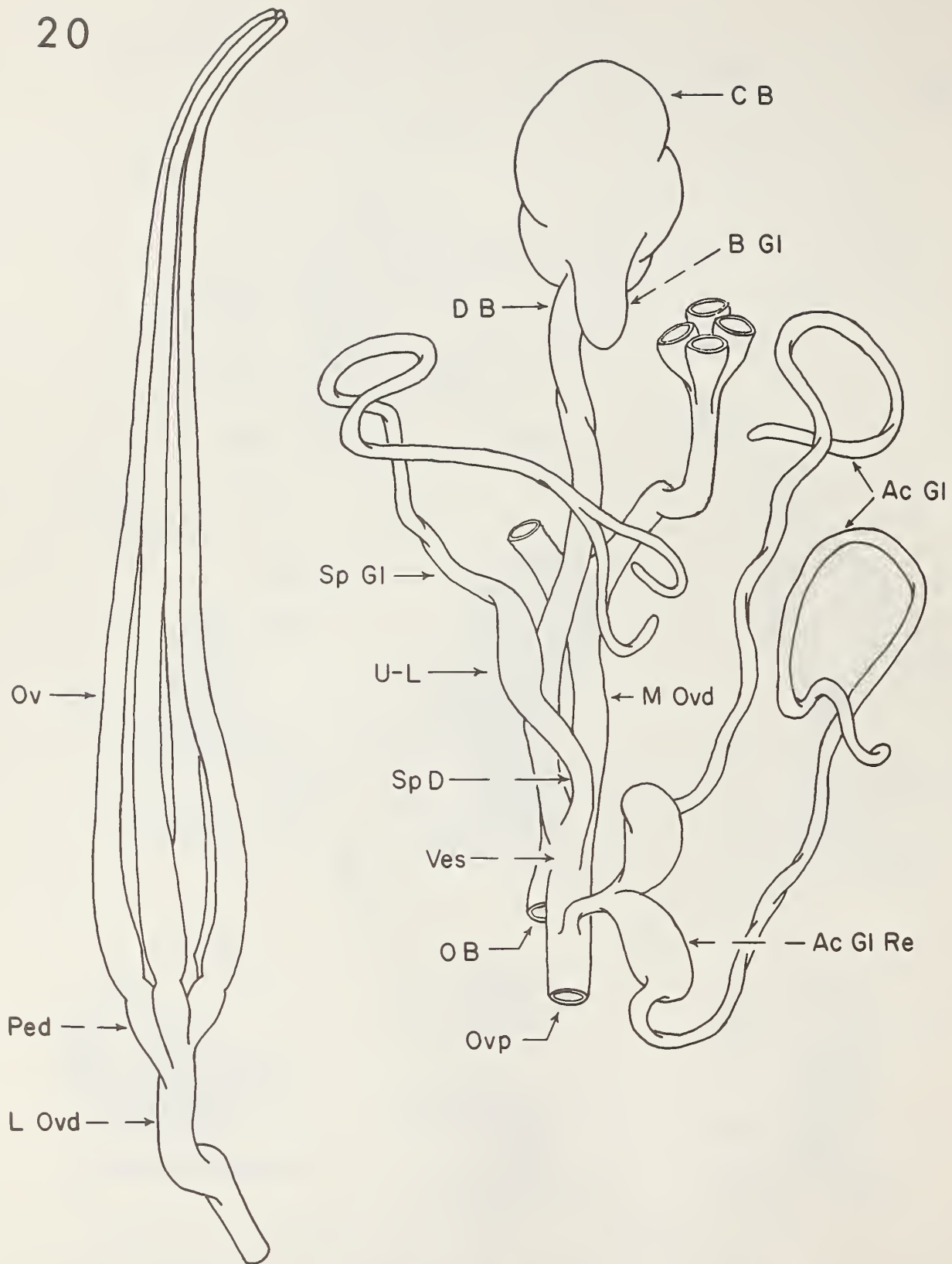
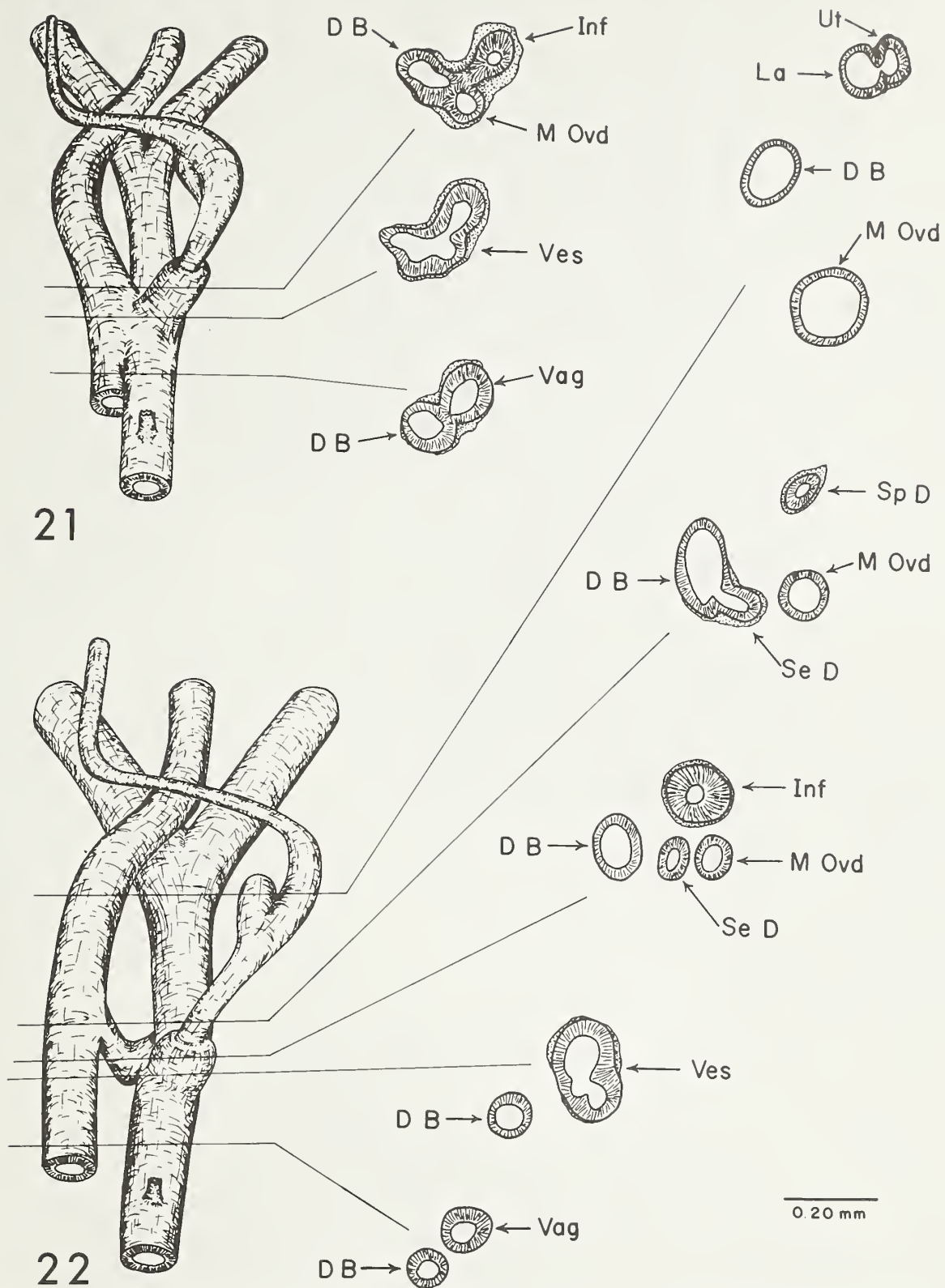


Figure 20.—36-Hour pupa, diagrammatic dorsal view. Organs spread slightly and right ovary omitted.

Legend: AcGl, accessory gland; AcGlRe, accessory gland reservoir; BGl, bursal gland; CB, corpus bursae; DB, ductus bursae; LOvd, lateral oviduct; MOvd, median oviduct; OB, ostium bursae; Ov, ovariole; Ovp, oviporus; Ped, pedicel; SpD, spermathecal duct; SpGl, spermathecal gland; U-L, utriculus-lagena dilation of the spermathecal rudiment; Ves, vestibulum.



**Figure 21.**—36-Hour pupa, lower reproductive tract. Both figures reconstructed from serial sections. The thin lines represent the plane of the corresponding transverse sections. Outlines of the sections were traced from microprojected images.

**Figure 22.**—48 Hour pupa, lower reproductive tract. Both figures reconstructed from serial sections. The thin lines represent the plane of the corresponding transverse sections. Outlines of the sections were traced from microprojected images.

**Legend:** Both figures reconstructed from serial sections. The thin lines represent the plane of the corresponding transverse sections. Outlines of the sections were traced from microprojected images. DB, ductus bursae; Inf, infundibulum; La, lagena; MOvd, median oviduct; SeD, Seminal duct; SpD, spermathecal duct; Ut, utriculus; Vag, vagina; Ves, vestibulum.

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